FIRST RECORD OF THE MARINE TARDIGRADE GENUS *BATILLIPES* (ARTHROTARDIGRADA: BATILLIPEDIDAE) FROM SOUTH AUSTRALIA WITH A DESCRIPTION OF A NEW SPECIES

R. M. KRISTENSEN AND B. S. MACKNESS

DEDICATION: **To the late Alan Bird who provided the first illuminating studies on South Australian tardigrades.**

KRISTENSEN, R. M. & MACKNESS, B. S. 2000. First record of the marine tardigrade genus *Batillipes* (Arthrotardigrada: Batillipedidae) from South Australia with a description of a new species. *Records of the South Australian Museum* **33**(2): 73–87.

A new species of marine tardigrade, *Batillipes lesteri* sp. nov. is described from beach sand collected at below low tide at Henley Beach, Adelaide, South Australia. Eighteen specimens including both sexes, four-toed larvae and juveniles were recovered. The new species differs from all other members of the Batillipedidae by its combination of toe patterns, fourth lateral projections and caudal apparatus. It is the first member of the genus to be described from South Australia and only the third species to be recorded from the Southern Hemisphere.

Reinhardt M. Kristensen, Invertebrate Zoology Department, University of Copenhagen, Universitetparken 15, DK-2100, Copenhagen, Denmark. Brian S. Mackness* School of Biological Sciences, James Cook University, Townsville, Qld, 4811. *Current address: PO Box 560 Beerwah, Queensland, Australia, 4519 (email: megalania@ compuserve.com). Manuscript received 1 December 1999.

The interstitial heterotardigrade genus *Batillipes* was first described by Richters (1909) based on specimens of *B. mirus* from Kieler Bay, in the Baltic Sea. Eight years later, Hay (1917) described *B. caudatus* obtained from algae from jetties at Beaufort, North Carolina. This American species was later incorrectly synonymised by Marcus (1929) with *B. mirus*. Marcus (1946) described a third species, *B. pennaki* from the Atlantic coasts of North and South America. Since that time many more new species have been discovered and named: *B. similis* Schulz, 1955; *B. carnonensis* Fize, 1957; *B. littoralis, B. phreaticus* Renaud-Debyser, 1959; *B. friaufi* Riggin, 1962; *B. annulatus,* De Zio 1962; *B. bullacaudatus* McGinty and Higgins, 1968; *B. gilmartini* McGinty, 1969; *B. dicrocercus* Pollock, 1970; *B. acaudatus, B.tubernatis* Pollock, 1971*; B. noerrevangi, B. roscoffensis* Kristensen, 1978; *B. adriaticus* Grimaldi de Zio *et al.*, 1979; *B. africanus, B. marcelli* Morone De Lucia *et al.*, 1988; *B. tridentatus* Pollock, 1989; *B. crassipes* Tchesunov and Mokievsky, 1995; *B. philippinensis, B. longispinosus* and *B. orientalis* Chang and Rho, 1997a,b. Most recently, Rho *et al.* 1999 described a new species *B. rotundiculus* and provided a key to eight batillipedid tardigrades from Korea.

Mackness (1999) recorded the first Australian members of *Batillipes* from beaches in Victoria but was unable to identify the animals to species level due to poor preservation. This paper presents the first record of the genus from South Australia and describes a new species based on 18 specimens collected subtidally from a beach in South Australia. Furthermore, the paper describes its life cycle including the four-toed larva, juveniles, young adults as well as their sexual dimorphism.

MATERIALS AND METHODS

Two sand samples (2 x 750 ml approx.) were collected on 6 November, 1995 by one of us (BM) at Henley Beach, Adelaide, South Australia (34° 55'S, 138° 30'E). One sample (A1) was taken at the low tide level and the other (A2), was taken at one metre water depth (subtidal). Tardigrades were only obtained from the subtidal sample. The tardigrades were sorted out alive at the Queensland Museum by RMK, two days after they were received. Each sample was fresh-water 'shocked' following the procedure set out by Kristensen and Higgins (1984). This involved soaking the sediments in fresh water for about 20

seconds and then swirling them around. This osmotically incapacitated the tardigrades which were collected after the heavier material had settled by decanting off the liquid through a 63 µm mesh filter. The meiofauna was sorted using a binocular microscope (40–80 x magnifications) and then examined using phase contrast microscopes (1000 x magnifications). A few tardigrades were removed and placed in sea water where they quickly recovered. All drawings were made using camera-lucida techniques on live animals. The reason for using live material for illustrations is that the lipoid eyes and the hard structures in the pharyngeal disappear in all known permanent mounts.

Live tardigrades adhering with their suction discs to the cover glass were then preserved in 2% buffered formalin added under the cover glass. Permanent mounts were made by adding specimens to a glycerine solution (4%) under cover glasses. After two days dehydration, the cover glasses were ringed with Glyceel. Measurements were only made on permanent mounts and taken to the nearest micron using an ocular micrometer. Comparisons were made with reference collections held in the Zoological Museum of the University of Copenhagen (ZMUC) and with original type descriptions from the literature. Measurements for 12 specimens are provided in Tables 1–3.

Systematics

Order Arthrotardigrada Marcus, 1927

Family BATILLIPEDIDAE Ramazzotti, 1962

Revised family diagnosis

Arthrotardigrade with large median cirrus present and secondary clava dome-shaped. Lateral cirrus and primary clava with a common pedestal. Internal cirrus and median cirrus with well-developed cirrophorus, external cirrus with indistinct cirrophorus. All cephalic cirri without scapus and flagellum. With four toes (in larvae) or six toes (in adults) of different lengths, with adhesive or suction disc at terminus of toe stalk. Claws absent. Cuticular seminal receptacles absent.

Discussion

This family had originally included the genera *Batillipes* and *Orzeliscus* Marcus. In this paper the family Orzeliscidae is considered as a sister group of the family Halechiniscidae and not the Batillipedidae. The Batillipidedae is therefore currently regarded as generically monotypic.

Batillipes Richters, 1909

Generic diagnosis

As Batillipedidae is monogeneric, the generic diagnosis is the same as that for the family.

Type species: Batillipes mirus Richters, 1909 by monotypy.

Type locality: Kieler Bay, Baltic Sea.

Discussion

The original description of *B. mirus* was written in German and perhaps this is the reason that this excellent early description has been overlooked. *Batillipes mirus* is a very large arthrotardigrade up to 720 µm (mean = 400–600 µm) with spade-shaped suction discs, similar to those of *B. tubernatis* illustrated by McKirdy (1975). The type material of *B. mirus* was collected subtidally (20 m water depth) and not in sandy beaches as nearly all later records for *B. mirus* worldwide. In the comprehensive review by McKirdy (1975) of the genus *Batillipes*, six species were examined carefully. The American '*B. mirus*' is a middle-sized batillipedid (about 160 µm) with ovoid or round suction discs. It is very clear that these animals are not the same as the type species. It may well be that all tidal animals called '*B. mirus*' are in fact *B. caudatus* described by Hay (1917) from North Carolina. This species was later incorrectly synonymised by Marcus (1929) with *B. mirus*. The cosmopolitan distribution (Table 4) of *B. mirus* must therefore be considered doubtful and new, worldwide samplings are necessary.

Batillipes lesteri n. sp.

(Figs 1–3, Tables 1–3)

Material examined

6 females, 5 males, 4 juveniles and 3 four-toed larvae collected sublittorally (1 m in water depth from the mean low tide), medium coarse sand from Henley Beach, Adelaide, South Australia. The sand samples were collected by B.M. on 6 November 1995. Holotype and seven paratypes will be deposited in the Queensland Museum. The other paratypes will be deposited in the Zoological Museum of the University of Copenhagen (ZMUC). Only 14 specimens were measured. In this paper, only the measurements of 12 specimens are given.

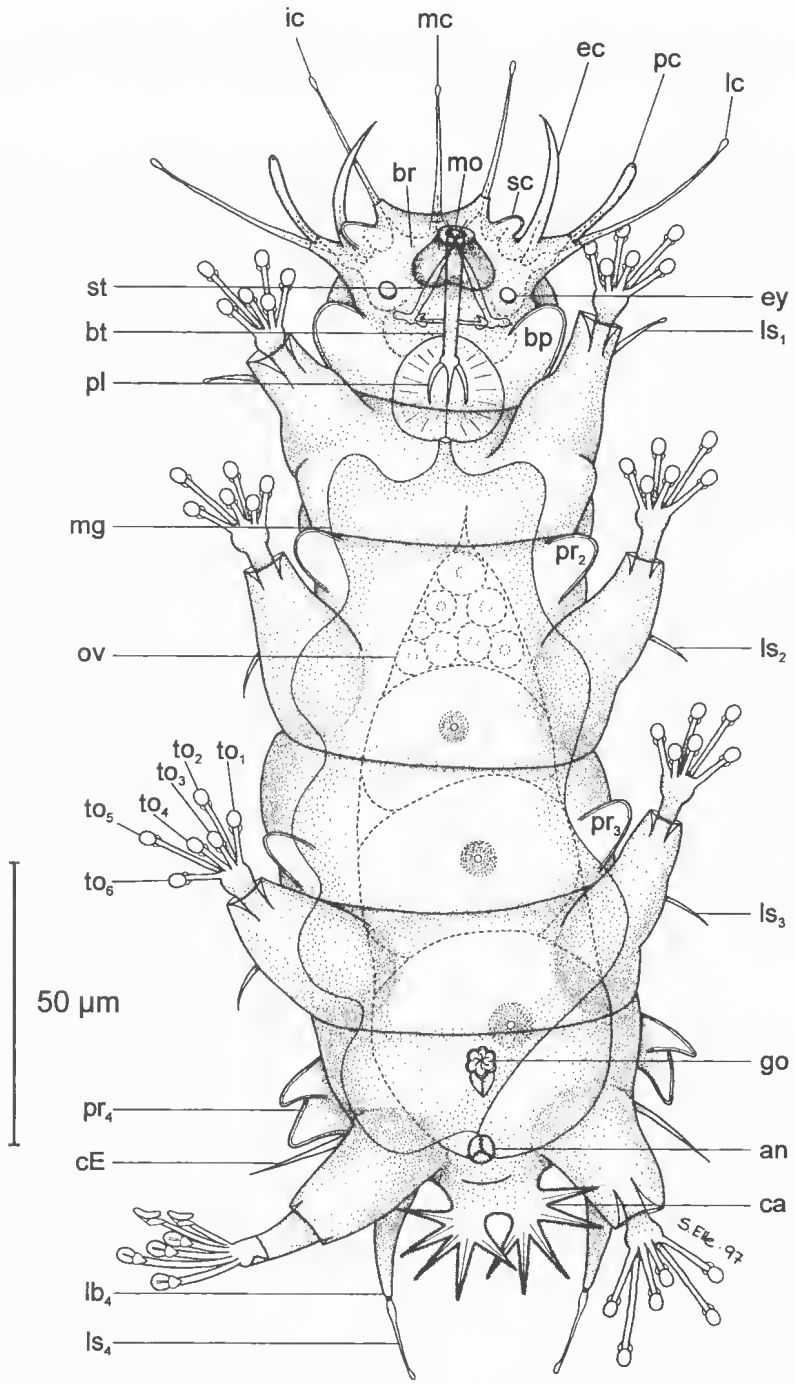

FIGURE 1. *Batillipes lesteri* n. sp. Holotypic female, ventral view. Scale bar equals 50 µm. Abbreviations: an, anus; bl, body length; bp, buccal projection; br, brain; bt, buccal tube; bw, body width; ca, caudal appendage; cE, cirrus E; ec, external cirrus; ey, eye; go, gonopore; ic, internal cirrus; lb_4, the base of leg IV sensory structure; ls_1-ls_3, leg I to leg III spines; ls_4, the spine of leg IV sensory structure; mc, median cirrus; mg, midgut; mo, mouth; oo, oocyte; ov, ovary; pc, primary clava; pl, placoid; pr_2–pr_4, lateral projections; sc, secondary clava; sl, stylet length; ss, stylet support; sv, seminal vesicle; te, testis; to_1-to_6, toe 1 to toe 6.

TABLE 1. Morphometry of *Batillipes lesteri* n. sp. Females. All measurements to the nearest micron.

Specimen	**Holotype Female** (Specimen 1)	**Female 2** large eyes (Specimen 4)	**Female 3** Part. destroyed (Specimen 5)	**Female 4** Immature (Specimen 6)
Body length	178.2 (178)	142.2 (142)	162.5 (163)	115.8 (116)
Body width	72.8 (73)	65.8 (66)	63.8 (64)	49.7 (50)
Buccal tube	25.0 (25)	23.7 (24)	22.0 (22)	20.2 (20)
Stylet length	23.1 (23)	22.5 (23)	20.8 (21)	19.5 (20)
Stylet support	6.0 (6)	6.0 (6)	5.8 (6)	4.8 (5)
Placoid	7.2 (7)	7.2 (7)	7.0 (7)	6.0 (6)
Median cirrus	27.7 (28)	24.4 (24)	25.2 (25)	19.2 (19)
Internal cirrus	29.7 (30)	25.3 (25)	25.5 (26)	21.3 (21)
External cirri	23.2 (23)	17.8 (18)	18.9 (19)	13.8 (14)
Lateral cirri	37.8 (38)	35.6 (36)	35.3 (35)	29.4 (29)
Primary clavae	14.5 (15)	14.9 (15)	12.7 (13)	12.2 (12)
Second. clavae	5.6 (6)	5.1 (5)	5.2 (5)	6.1 (6)
Cirri E	23.2 (23)	21.5 (22)	24.4 (24)	21.0 (21)
Leg IV base	23.1 (23)	19.2 (19)	18.3 (18)	13.4 (13)
Leg IV spine	16.5 (17)	15.0 (15)	15.8 (16)	12.2 (12)
Leg III spine	13.0 (13)	12.1 (12)	10.2 (10)	10.4 (10)
Leg II spine	12.5 (13)	11.9 (12)	10.1 (10)	10.0 (10)
Leg I spine	10.0 (10)	10.5 (11)	9.7 (10)	9.5 (10)
Buccal project.	9.9 (10)	7.7 (8)	8.2 (8)	7.5 (8)
Projection 2	12.5 (13)	8.1 (8)	11.4 (12)	8.9 (9)
Projection 3	13.2 (13)	10.3 (10)	12.3 (12)	9.5 (10)
Projection 4	15.3 (15)	15.2 (15)	13.1 (13)	11.7 (12)
Caudal apparatus	21.0 x 26.4	16.8 x 19.2	20.0 x 15.0	16.0 x 12.9
apparatus (width x length)	(21 x 26) bilobed, each with 5 spikes	(17 x 19) bilobed, each with 3 spikes	(20 x 15) bilobed, each with 3 spikes	(16 x 13) bilobed, each with 4 spikes
Leg 1 (toe 1)	9.5 (10)	9.5 (10)	9.5 (10)	9.5 (10)
(toe 2)	5.9 (6)	5.7 (6)	5.6 (6)	5.2 (5)
(toe 3)	12.5 (13)	14.1 (14)	12.8 (13)	12.0 (12)
(toe 4)	7.9 (8)	7.8 (8)	7.9 (8)	7.2 (7)
(toe 5)	17.1 (17)	17.2 (17)	16.1 (16)	15.0 (15)
(toe 6)	10.5 (11)	9.8 (10)	9.8 (10)	10.0 (10)
Leg IV (toe 1)	13.8 (14)	12.9 (13)	12.4 (12)	10.8 (11)
(toe 2)	19.8 (20)	17.0 (17)	18.4 (18)	15.2 (15)
(toe 3)	8.5 (9)	7.5 (8)	7.8 (8)	5.8 (6)
(toe 4)	13.2 (13)	11.7 (12)	11.3 (11)	10.2 (10)
(toe 5)	22.4 (22)	18.2 (18)	21.5 (22)	16.0 (16)
(toe 6)	13.4 (13)	10.6 (11)	11.8 (12)	9.8 (10)
Gonopore/Anus	11.0 (11)	11.2 (11)	10.2 (10)	rosette not present
Ovary	3 eggs	2 eggs	2 eggs	immature
Toe formula	6-6-6-6	6-6-6-6	6-6-6-6	6-6-6-6

Diagnosis

Middle-sized *Batillipes* with large lipoid eyes, swollen tips on lateral, internal and median cirri as well as on fourth leg spine; enlarged fourth leg spine with a van der Land body separating the cirrophore from spinous part of the leg sense organ. The prominent lateral projection between legs III and IV is two-pointed in adults and juveniles, one-pointed in larvae. The caudal apparatus is an ala-like structure with thin cuticular fibres often covered with detritus. This structure varies extremely from simple bilobed to highly furcated (4–10 spikes). Slightly sexually dimorphic (females larger than males); females with wider gonopore-anus distance than males, and females with two-valved cuticular structures associated with the rosette gonopore system. Uneven 3rd (short) and 4th (long) toe on fourth leg, all toes with ovoid suction discs.

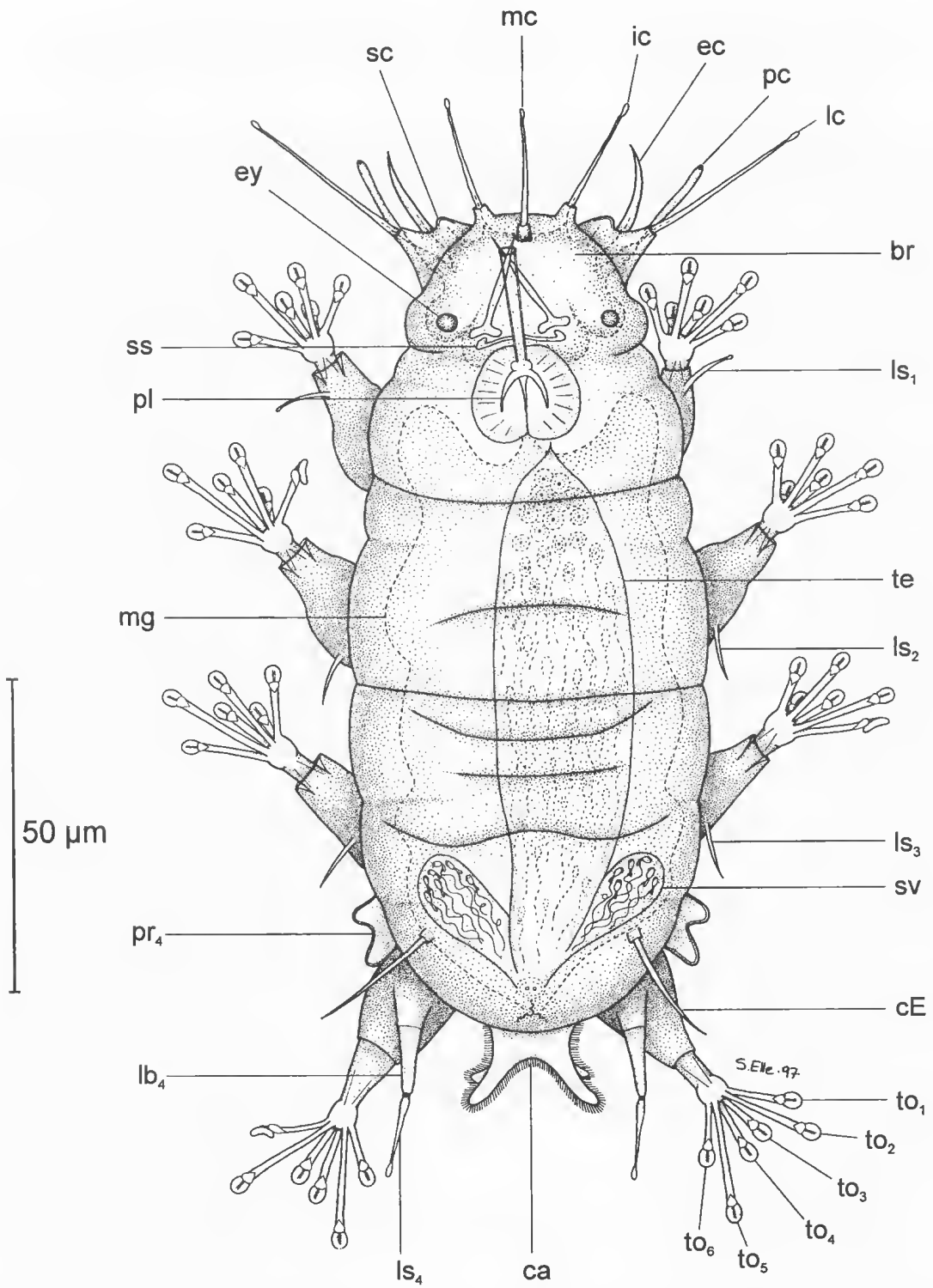

FIGURE 2. *Batillipes lesteri* n. sp. Allotypic male, dorsal view. Scale bar equals 50 µm. Abbreviations as for Fig. 1.

TABLE 2. Morphometry of *Batillipes lesteri* n. sp. Males. All measurements to the nearest micron.

Specimen	**Allotypic male** (Specimen 2)	**Male 2** vent./gonopore (Specimen 7)	**Male 3** lateral (Specimen 8)	**Male 4** 1mm. Testis (Specimen 9)
Body length	133.7 (134)	174.2 (174)	129.0 (130)	112.5 (113)
Body width	66.8 (67)	73.5 (73)	lateral view	47.8 (48)
Buccal tube	21.7 (22)	21.8 (22)	18.8 (19)	17.1 (17)
Stylet length	19.8 (20)	21.0 (21)	17.5 (18)	15.3 (15)
Stylet support	5.9 (6)	6.2 (6)	5.3 (5)	5.2 (5)
Placoid	6.6 (7)	7.1 (7)	7.0 (7)	6.0 (6)
Median cirrus	23.0 (23)	28.1 (28)	22.8 (23)	19.8 (20)
Internal cirrus	23.1 (23)	28.9 (29)	23.0 (23)	22.2 (22)
External cirri	19.8 (20)	19.6 (20)	15.4 (15)	14.9 (15)
Lateral cirri	31.5 (32)	38.9 (39)	32.5 (33)	33.1 (33)
Primary clavae	13.8 (14)	15.0 (15)	13.0 (13)	11.7 (12)
Second. clavae	5.2 (5)	5.3 (5)	5.1 (5)	4.9 (5)
Cirri E	21.1 (21)	22.5 (23)	21.0 (21)	20.2 (20)
Leg IV base	18.3 (18)	17.8 (18)	13.5 (14)	15.6 (16)
Leg IV spine	15.8 (16)	18.0 (18)	12.8 (13)	13.3 (13)
Leg III spine	10.5 (11)	13.2 (13)	10.2 (10)	9.8 (10)
Leg II spine	10.5 (11)	12.1 (12)	9.8 (10)	9.4 (9)
Leg I spine	9.5 (10)	12.0 (12)	8.9 (9)	9.1 (9)
Buccal project.	8.0 (8)	9.5 (10)	6.2 (6)	7.2 (7)
Projection 2	9.8 (10)	10.8 (11)	7.5 (8)	9.5 (10)
Projection 3	10.3 (10)	12.2 (12)	8.0 (8)	10.2 (10)
Projection 4	11.8 (12)	15.8 (16)	13.4 (13)	12.9 (13)
Caudal apparatus (width x length)	16.2 x 17.8 (16 x 18) bilobed, each with 2 spikes	15.8 x 16.0 (16 x 16) bilobed, each with 2 spikes	11.5 x 13.0 (12 x 13) bilobed, each with 2 spikes	15.0 x 13.2 (15 x 13) bilobed, each with 2 spikes
Leg 1 (toe 1)	9.9 (10)	10.1 (10)	8.5 (9)	7.2 (7)
(toe 2)	5.9 (6)	6.0 (6)	5.0 (5)	4.9 (5)
(toe 3)	12.5 (13)	15.3 (15)	13.8 (14)	11.9 (12)
(toe 4)	7.9 (8)	9.2 (9)	8.2 (8)	6.1 (6)
(toe 5)	17.1 (17)	18.5 (19)	15.0 (15)	15.2 (15)
(toe 6)	9.2 (9)	11.6 (12)	9.8 (10)	8.0 (8)
Leg IV (toe 1)	12.5 (13)	14.1 (14)	10.2 (10)	10.1 (10)
(toe 2)	18.4 (18)	19.4 (19)	15.8 (16)	14.7 (15)
(toe 3)	8.5 (9)	7.5 (8)	6.2 (6)	5.2 (5)
(toe 4)	11.5 (12)	12.6 (13)	10.1 (10)	10.0 (10)
(toe 5)	21.0 (21)	21.7 (22)	18.2 (18)	15.3 (15)
(toe 6)	11.2 (11)	11.8 (12)	9.4 (9)	9.2 (9)
Gonopore/Anus	3.3 (3)	4.2 (4)	3.0 (3)	2.9 (3)
Testis	mature sperm	mature sperm	without seminal vesicles	without seminal vesicles
Toe formula	6-6-6-6	6-6-6-6	6-6-6-6	6-6-6-6

Description

Holotype

Adult female (Fig. 1) with body 178 µm long measured excluding caudal appendage and 73 µm wide between legs II and III. Head distinguished from body by a constriction beneath lateral cirri and primary clavae. Head width 45 µm between bases of lateral cirri. Median cirrus unpaired, with large cirrophore and swollen tip (28 µm). Internal cirri also with large cirrophores and swollen tips (30 µm) directed anteriorly. External cirri horn-shaped (23 µm long) with indistinct cirrophores. Primary clavae moderately long (15 µm), thick and tube-shaped. Primary clava and lateral cirrus with a common pedestal (cirrophore of lateral cirrus). Primary clava with a thick cuticular annulus (van der Land body) inside base. Lateral

TABLE 3. Morphometry of *Batillipes lesteri* n. sp. Larva and Juveniles. All measurements to the nearest micron.

Specimen	**Four-toed larva** (Fig. 3) (First instar) (Specimen 3)	**Four-toed larva 2** (First instar) (Specimen 10)	**Juvenile 2** (Third instar) (Specimen 11)	**Juvenile 3** (Fourth instar) (Specimen 12)
Body length	76.5 (77)	78.5 (79)	85.8 (86)	105.2 (105)
Body width	29.7 (30)	27.9 (28)	29.7 (30)	43.8 (44)
Buccal tube	16.5 (17)	15.7 (16)	simplex	18.2 (18)
Stylet length	13.8 (14)	15.2 (15)	simplex	16.5 (17)
Stylet support	3.9 (4)	3.8 (4)	simplex	5.0 (5)
Placoid	4.6 (5)	4.2 (4)	simplex	6.3 (6)
Median cirrus	19.5 (20)	18.2 (18)	20.2 (20)	19.1 (19)
Internal cirrus	20.4 (20)	18.9 (19)	21.1 (21)	20.3 (20)
External cirri	10.5 (11)	10.2 (10)	13.2 (13)	14.4 (14)
Lateral cirri	29.7 (30)	28.9 (29)	29.7 (30)	30.7 (31)
Primary clavae	9.5 (10)	9.0 (9)	9.9 (10)	12.6 (13)
Second. clavae	2.6 (3)	3.7 (4)	3.3 (3)	5.0 (5)
Cirri E	19.8 (20)	19.0 (19)	19.1 (19)	20.1 (20)
Leg IV base	9.2 (9)	10.2 (10)	8.5 (9)	12.8 (13)
Leg IV spine	9.2 (9)	9.8 (10)	8.7 (9)	13.0 (13)
Leg III spine	9.9 (10)	9.5 (10)	9.2 (9)	9.3 (9)
Leg II spine	9.9 (10)	9.2 (9)	9.0 (9)	9.0 (9)
Leg I spine	8.5 (9)	8.0 (8)	8.7 (9)	8.7 (9)
Buccal project.	5.9 (6)	5.0 (5)	5.9 (6)	5.8 (6)
Projection 2	6.6 (7)	6.2 (6)	5.9 (6)	6.2 (6)
Projection 3	7.2 (7)	7.4 (7)	7.9 (8)	6.7 (7)
Projection 4	8.5 (9)	10.0 (10)	9.9 (10)	9.1 (9)
Caudal apparatus (width x length)	6.2 x 4.6 (6 x 5) bilobed, each with one spike	8.2 x 10.5 (8 x 11) bilobed with blunt tip	6.8 x 5.2 (7 x 5) bilobed, each with two small spikes	11.2 x 12.7 (11 x 12) bilobed, each with two spikes
Leg 1 (toe 1)	5.2 (5)	5.2 (5)	5.2 (5)	8.2 (8)
(toe 2)	0	0	0	4.9 (5)
(toe 3)	11.2 (11)	12.1 (12)	7.9 (8)	13.7 (14)
(toe 4)	5.2 (5)	6.8 (7)	5.9 (6)	7.0 (7)
(toe 5)	0	0	9.9 (10)	15.0 (15)
(toe 6)	7.2 (7)	8.2 (8)	7.6 (8)	9.6 (10)
Leg IV (toe 1)	7.9 (8)	7.2 (7)	9.9 (10)	9.1 (9)
(toe 2)	14.2 (14)	14.0 (14)	13.2 (13)	15.8 (16)
(toe 3)	0	0	4.6 (5)	5.7 (6)
(toe 4)	0	0	7.9 (8)	9.2 (10)
(toe 5)	11.2 (11)	10.1 (10)	14.5 (15)	16.4 (16)
(toe 6)	8 .2 (8)	8.0 (8)	9.2 (9)	9.0 (9)
Gonopore/Anus	lacking	lacking	gonopore lacking/ anus present	gonopore lacking/ anus present
Toe formula	4-4-4-4	4-4-4-4	5-6-6-6	6-6-6-6

cirri long and tapered terminating in prominent swelling (38 µm). Secondary clavae (base 6 µm) located between internal and external cirri at frontal edge of head. Two large lipoid eyespots present only in live animal consisting of one very large ball-shaped lipoid droplet. The hyalin spherical structure is seen on the inside of the external brain lobe (protocerebrum). It is supposed they are of lipid composition based on their solubility in alcohol and glycerol. Pharyngeal bulb subcircular (18 µm x 21 µm) located between legs I. In optical cross-section, bulb is trilobate, each lobe with a calcium carbonate encrusted placoid (7 µm). Buccal tube straight and moderately long (25 µm) with (3 µm) width. Buccal tube extends inside pharyngeal bulb attaching placoids via three

apophyses. Ventral mouth as in characteristic pouting in typical *Batillipes* form (*sensu* Kristensen 1978). Stylet supports straight (6 µm) with support knob showing slight deflection anteriorly. Support knobs linked on large furca of stylet. Stylets length 23 µm.

Spines present on all legs. Spine of legs I located more distally than all other spines. Spines on legs II–IV located proximally to body. Increasing size of spines from legs I–IV, 10.0 µm, 12.5 µm, 13.0 µm, 16.5 µm + 23.1 µm respectively. Fourth leg spine very long with large base (cirrophore) and a cuticular annulus (van der Land body) separating base from spine which is the true sense organ. Total length of whole fourth leg sensory structure 49.6 µm. First and fourth leg spines with swollen tips as in cephalic cirri. Cirri E moderately long (23 µm) and sharply pointed with distinct cirrophore. Ventral tongue-shaped projections in front of leg I (10 µm), leg II (13 µm long) and leg III (13 µm long). Lateral projection in front of leg IV bifurcate (15 µm long). Caudal apparatus ala-like and strongly furcated (2 x 5 spikes). Cuticle of caudal apparatus has fine hairs; it is covered with bacteria and detritus. Gonopore rosette-shaped with six identical segments. Behind the female gonopore there is a two valved cuticular structure. Gonopore-anus distance is 11 µm. The holotypic female is sexually mature, with three large eggs.

Legs I–IV possessing toes of varying lengths. On leg I, toe 5 is the longest (17 µm) with toes decreasing in size 3, 6, 1, 4 and 2 (13 µm, 11 µm, 8 µm and 6 µm respectively). On legs IV, toes 2 and 3 are unequal in size and conform to toe pattern D (see Table 5). Length of toes in decreasing order of size is 5, 22 µm; 2, 20 µm; 1, 14 µm; 4, 13 µm; 6, 11 µm and 3, 9 µm. Toe discs ovate with conspicuous brace.

Allotype

Adult male (Fig. 2) with body 134 µm long measured excluding caudal appendage, and 67 µm wide between legs II and III. Male is similar to female except for size and differences in shape of projection in front of leg IV which is slightly bilobate, and caudal appendage lobate with only four spikes. Gonopore-anus distance is only 3 µm, meaning that the gonopore nearly connects the anterior branch of a three-lobed anal system. Male gonopore located on a small ovoid papilla. The allotype is sexually mature with two lateral seminal vesicles filled with mature spermatozoa.

The allotype is drawn in dorsal perspective. Dorsal transverse lines indicating segmental plates disappear after fixation. The punctations of the dorsal cuticle (see McKirdy 1975) are very coarse, especially laterally, where the epicuticular pillars, which form the punctations, can be seen using light microscopy. Each lateral pillar is about 2 µm high.

Four-toed larva

The first instar of all species of *Batillipes* is so different from subsequent instars, that the term 'larva' (*sensu* Bertolani *et al.* 1984) is correct. The paratypic larva illustrated (Fig. 3, Table 3) has a body length of 77 µm and body width of 30 µm. It shows typical ontogenetic body proportions with a larger head region in relation to body, lacks the gonopore, the anus is only a slit, and it is not three-lobed. The larva has only four toes instead of the six toes of the adult. Toe 2 and 5 are missing on legs I–III and toes 3 and 4 are missing on leg IV. The leg spines I–III are with a swollen tip, but the leg spine IV is pointed. The projection 4 has only one spike and the caudal appendage is only slightly bilobed.

Juvenile

The animals without gonopore, but with three-lobed anus are called juveniles. At least two instars can be recognized but they could be more numerous. The second instar has the toe formula 5-5-5-6 and the third instar has 5-6-6-6. All sense organs have the characteristics of the adult, but the projection in front of leg IV and the caudal apparatus vary a lot. The differences between males and females can be seen in the size and especially in the caudal apparatus.

Young adults

Animals with gonopores, but with immature reproductive systems are called young females and males. These animals are smaller in size, but are still sexually dimorphic. The young males lack the seminal vesicles with mature spermatozoa while the young females have only small-size oocytes in the ovaries.

Life Cycle

There is no doubt that *B. lesteri* was in the middle of its reproductive cycle when the specimens were collected in November, which is the last month in the Australian Spring. It is unusual to have so many four-toed larvae and juveniles in populations of *Batillipes*. The first instar, the four-toed larva, differed dramatically from the juveniles and adults. It is difficult to interpret just how many instars are involved

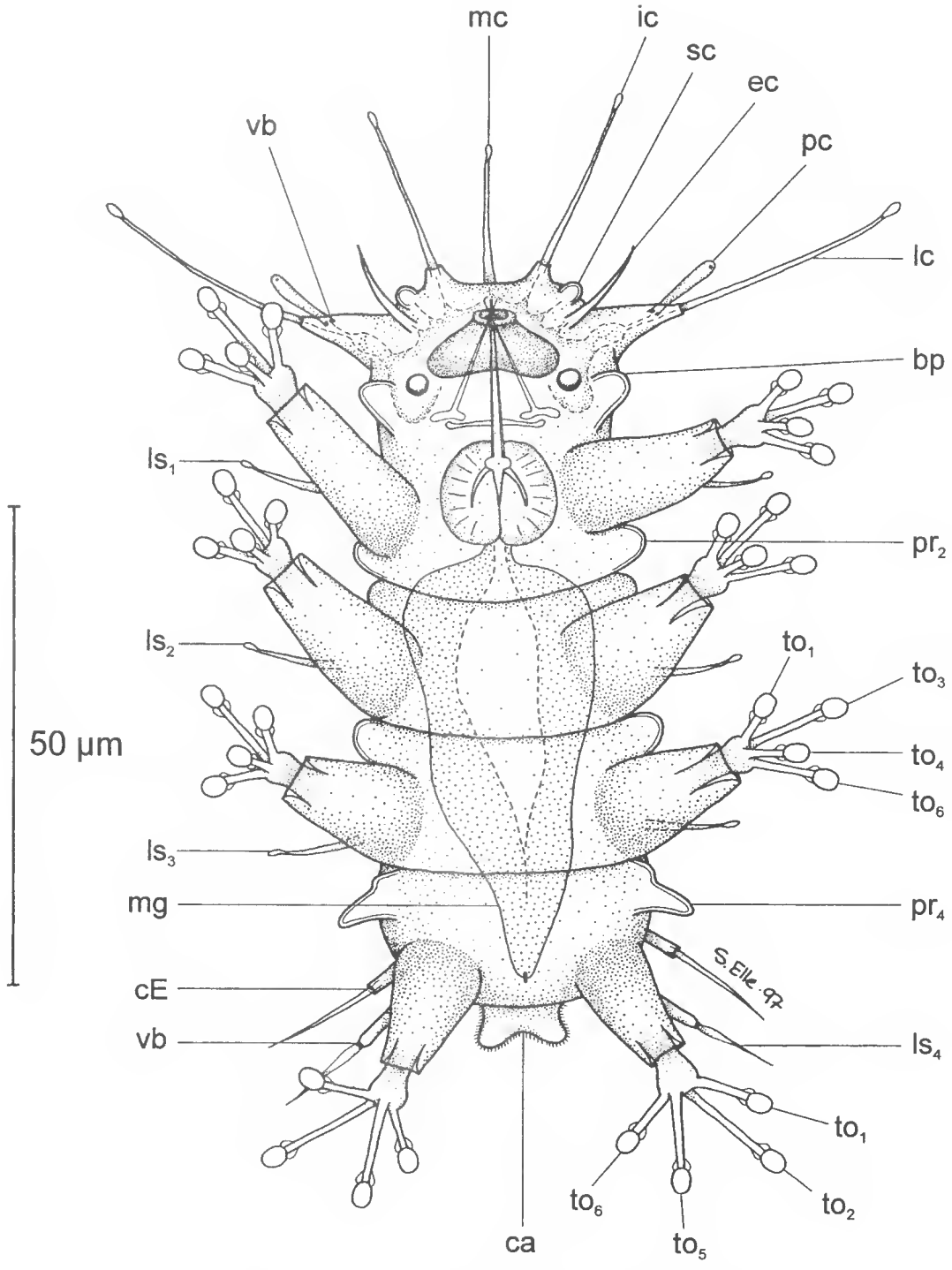

FIGURE 3. *Batillipes lesteri* n. sp. Paratypic four-toed larva. Scale bar equals 50 µm. Abbreviations as for Fig. 1.

TABLE 4. Zoogeographic distribution of species of the genus *Batillipes*. (Southern hemisphere records in bold).

B. acaudatus – England (Pollock, 1971)
B. adriaticus – Italy – (Grimaldi De Zio *et al.*, 1979)
B. africanus – Libéria (Morone De Lucia *et al.*, 1988)
B. annulatus – Italy (De Zio 1962, Grimaldi De Zio *et al.* 1979)
B. bullacaudatus – USA (McGinty & Higgins 1968, Pollock 1970b; Lindgren 1971; McKirdy 1975); Scotland (McIntyre & Murison 1973)
B. carnonensis – France (Fize 1957); Italy (Grimaldi De Zio *et al.* 1980, 1983); USA (Fleeger 1978)
B. crassipes – Russia (Tchesunov & Mokievsky 1995); Korea (Rho *et al.* 1999)
B. dicrocercus – USA (Pollock 1970a, McKirdy 1975, Hummon 1994); Italy (Hummon 1994; Grimaldi De Zio *et al.* 1980, D' Addabbo Gallo *et al.* 1987, Matarrese *et al.* 1996); Poland (Hummon 1994)
B. friaufi – USA (Riggin 1962, McKirdy 1975, Gaugler & Nelson 1997)
B. gilmartini – USA (McGinty 1969. Pollock 1989)
B littoralis – France (Renaud-Debyser 1959, D'Hondt 1970, Renaud-Debyser & Salvat 1963); Italy (Grimaldi De Zio *et al* . 1983, D'Addabbo Gallo *et al* 1987, D'Addabbo Gallo *et al.* 1999, Grimaldi De Zio *et al.* 1999)
B. longispinosus – Korea (Chang & Rho 1997a, Rho *et al.* 1999)
B. marcelli – Italy (Morone De Lucia *et al.* 1988)
B. mirus – Germany (Richters 1909); Wales (Boaden 1963); Ireland (Boaden 1966); Scotland (Pollock 1971; McIntyre & Murison 1973); Norway (Tambs-Lyche 1939–40); Denmark (Fenchel *et. al* 1967, Fenchel 1969, Kristensen 1978); Finland (Purasjoki 1953, Karling 1954–1955); Sweden (Jägersten 1952); North Sea (Remane 1940, Freidrich 1963); Black Sea (Plesa 1963); Germany (Schmidt 1969) Bulgaria (Valkanov 1950, 1954); Romania (Rudescu 1964); Russia (Petelina & Tchesunov 1983, Biserov 1991); France (Baudoin 1952, Swedmark 1956 a,b, Renaud- Debyser 1956, Guérin 1960, Renaud-Mornant & Jouin 1965; D'Hondt 1970,Renaud-Debyser & Salvat 1963); Italy (Papi 1952, D'Addabbo Gallo *et al.* 1987); **Madagascar (Renaud-Mornant 1979)**; USA (Hay 1917, King 1962, McGinty & Higgins 1968, Pollock 1970a, Lindgren 1971, McKirdy 1975, Meyer cited in Pollock 1989, Pollock 1989, Gaugler & Romano 1995, Gaugler & Nelson 1997); Bahamas (Pollock 1970b); **Malaysia (Renaud-Mornant & Serène 1967)**
B. noerrevangi – Denmark (Kristensen 1976, 1978)
B. orientalis – Korea (Chang & Rho 1997, Rho *et al.* 1999))
B. pennaki – Massachusctts, USA (Marcus 1946, Pollock 1970b, McKirdy 1975); **Brazil (Marcus 1946);** France (Renaud-Debyser 1959,Renaud-Debyser & Salvat 1963); Italy (De Zio 1962, 1964, Grimaldi de Zio & D'Addabbo Gallo 1975, Grimaldi De Zio *et al.* 1979, Bertolani *et al.* 1984, D'Addabbo Gallo *et al.* 1987); Spain (Villora-Mofeno & Grimaldi de Zio 1993); India (Rao & Ganapati 1968); Korea (Rho *et al.* 1999)
B. philippinensis – Philippines (Chang & Rho 1997b); Korea (Rho *et al.* 1999)
B. phreaticus – France (Renaud-Debyser 1959, Renaud-Debyser & Salvat 1963); Germany (Riemann 1966); England (Pollock 1971); Spain (Villora-Moreno & Grimaldi De Zio 1993); Italy (D'Addabbo *et al.* 1987).
B. roscoffensis – France (Kristensen 1978)
B. rotundiculus – Korea (Rho *et al.* 1999)
B. similis – Germany (Schulz 1955); Korea (Rho *et al.* 1999) France (Fize 1963); Italy (Grimaldi De Zio *et al.* 1980, D'Addabbo Gallo *et al.* 1999, Grimaldi De Zio *et al.* 1999)
B. tridentatus – Washington & California, USA (Pollock 1989); Korea (Rho *et al.* 1999)
B. tubernatis – Scotland (McIntyre & Eleftheriou 1968, Pollock 1971); Germany (Riemann 1966, Hummon 1994); USA (McKirdy 1975)

before an animal is sexually matured but at least four moults are present before the gonopore is seen. The following instars have been recorded for this species. First instar –the four toed larvae; Second instar – juvenile with toe formula 5-5-5-6; Third instar – juvenile with toe formula 5-6-6-6; Fourth instar juvenile without gonopore but with toe formula 6-6-6-6; Adult—with gonopore and three-lobed anus.

Etymology

Named in honour of curator Dr Lester R. G. Cannon, Queensland Museum, who facilitated our collaboration.

TABLE 5. Patterns of toe length on fourth foot of species of *Batillipes*. (Modified after Pollock 1970a)

A (III & IV equal)	B (I & III equal)	C (II & IV equal)	D (III & IV unequal)
B. acaudatus	*B. phreaticus*	*B. friaufi*	*B. africanus*
B. adriaticus		*B. littoralis*	*B. lesteri*
B. annulatus			*B. tubernatis*
B. bullacaudatus			*B. similis*
B. carnonensis			
B. crassipes			
B. dicrocercus			
B. gilmartini			
B. longispinosus			
B. marcelli			
B. mirus			
B. noerrevangi			
B. orientalis			
B. pennaki			
B. philippinensis			
B. roscoffensis			
B. rotundiculus			
B. tridentatus			

Systematic Discussion

Species of the genus *Batillipes* are amongst the most studied of all marine tardigrades. Their taxonomy remains problematic with relatively few characters commonly used in systematic investigations of the group (McKirdy 1975). Some of the characters used (e.g. conformation of lateral body projections, relative length and shape of cephalic appendages), are directly affected by the physical mounting process. Total body length and width may vary due to cover slip pressure; shrinkage can occur due to the mounting medium and lengths of spines and cirri may be miscalculated because of their orientation to the observer. Internal features such as eyespots and buccal apparatus can also be affected by mounting media and cover slip pressure. Apart from these mechanical problems, there are also a range of other factors to contend with. The caudal appendage of *Batillipes* has often been used in the diagnosis of species but various authors have shown this can vary ontogenetically (Grimaldi de Zio and D'Addabbo Gallo 1975; Morone De Lucia *et al.* 1988). Further ontogenetic variation has been recorded by Kristensen (1978), McGinty and Higgins (1968) and Villora-Morena and Grimaldi de Zio (1993).

Comparative studies have also been made difficult because of the inconsistent nomenclature of toes and the lack of a full range of specimens of both sexes, four-toed larvae and juveniles for many species. In this study, we have used the standard method of numbering toes on the fourth leg with toe 1 being the closest cranially on the right hand side and the toes then numbered sequentially in a clockwise direction. This makes the caudoproximal toe, toe 6 in our scheme (Table 5). Furthermore, the attachment of the toes to the tarsus has systematic value in determining which toe is missing in larvae and in juveniles. At leg 1, the 2nd and 4th toes are ventral, 1st and 6th lateral and 3rd and 5th dorsal on the tarsus. This distribution is functionally correct: the shortest toes are ventral and the longest dorsal.

The relative position of these toes, particularly those on right leg IV has been used as an important taxonomic indicator (Pollock 1970a). Even here problems can arise if the legs are not properly positioned or incorrectly illustrated. It is therefore necessary to have a range of specimens, of both sexes, including juveniles if any meaningful taxonomic decisions are to be made. *Batillipes lesteri* n. sp. differs from all other species of *Batillipes* by having uneven 3rd and 4th toes on leg IV except for *B. africanus, B. similis* and *B. tubernatis*. It differs from *B. tubernatis* by having a caudal apparatus with fine cuticular hairs and differs from *B. africanus* by the males having bilobate caudal appendages with four spikes and females having highly furcated (6–10 spikes) caudal appendages. It differs from *B. similis* by

having different primary clava as well as caudal and lateral processes.

Ontogenetic differences between other species of *Batillipes* are seen in the toe formula. Larvae of *B. noerrevangi* lack toe 2 (the smallest one of the adult) and toe 6 on leg I. Larvae of *B. lesteri* also lack toe 2 but instead of toe 6, they lack toe 5 (the longest toe in the adult) on leg I.

Marine tardigrades also go through a life cycle with a number of moults and will vary morphologically at different stages of this cycle including a process called cyclomorphosis (Kristensen 1982) Furthermore the species may vary in morphology according to differences in salinity (Kristensen 1978). A proper analysis of both sexual and ontogenetic variations is necessary in many instances before new taxa should be raised.

The new species of *Batillipes* is only the third recorded for the Southern Hemisphere. A zoogeographic analysis of the 24 species recorded so far (Table 4) shows a singular distributional bias towards the northern hemisphere. This is probably more an artefact of where marine tardigradologists have been working and collecting rather than any zoogeographic pattern. In this analysis, most *Batillipes* species are still primarily known from their type localities with only three species *B. mirus*, *B. pennaki* and *B. phreaticus* having more cosmopolitan distributions.

Several studies have shown that certain species of *Batillipes* live sympatrically occupying specific regions of the littoral environment (Renaud-Debyser 1959, Schmidt 1969, Lindgren 1971). Furthermore, Renaud-Debyser (1959) and Pollock (1975) have demonstrated that *Batillipes* shows tolerances and preferences to water content, temperature, light and salinity. This predicates that any understanding of the distribution of species of *Batillipes* at any location must take all these factors into account. Some beaches may have an almost monotypic batilliped fauna while others may support several species in different locations. Further ecological studies and collecting of Australian marine tardigrades is needed to clarify whether these patterns hold true in southern latitudes.

Acknowledgments

The authors wish to thank the Australian Biological Resources Study (ABRS), the whole curatorial staff and especially Dr Lester R. G. Cannon of the Queensland Museum for the provision of facilities and ABRS Fellowship during the one year stay (1995–1996) of one of us (RMK). Stine Elle and Aslak Jørgensen (ZMUC) undertook the illustrations, and their work was enabled by a grant to RMK from the Carlsberg Foundation (Grant No. 970345/30–488). Dr Susanna Grimaldi de Zio, Dr Leland Pollock and Dr Woody Horning Jr provided useful comments on the manuscript.

References

BAUDOIN, R. 1952. Contribution à l'écologie et à la biogéographie de la zone intercôtidale des Charentes. *Compte Rendu des Séances de la Société de Biogéographie*. **215:** 72–82.

BERTOLANI, R., GRIMALDI DE ZIO, S., D'ADDABBO GALLO, M. & MORONE DE LUCIA, M. R. 1984. Postembryonic development in heterotardigrades. *Monitore Zoologico Italiano* (N.S.) **18:** 307–320.

BISEROV, V. I. 1991. An annotated list of Tardigrada from European Russia. *Zoologische Jahrbücher, Abteilung für Systematik Ökologie und Geographie der Tiere* **118:** 193–216.

BOADEN, P. J. S. 1963. The interstitial fauna of some North Wales beaches. *Journal of the Marine Biological Association of the United Kingdom* **43:** 79–96.

BOADEN, P.J.S. 1966. Interstitial fauna from Northern Island. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* **2:** 125–130.

CHANG, C. Y. & RHO, H. S. 1997a. Two New Marine Tardigrades of Genus *Batillipes* (Heterotardigrada: Batillipedidae) from Korea. *Korean Journal of Systematic Zoology* **13:** 93–102.

CHANG, C. Y. & RHO, H. S. 1997b. Two New Marine Tardigrades from Palawan Island, the Philippines. *Korean Journal of Biological Science* **1:** 419–423.

D'ADDABBO GALLO, M., GRIMALDI DE ZIO S. & MORONE DE LUCIA, M. R., 1999. Diversity and dynamics of an interstitial Tardigrada population in the Meloria Shoals, Ligurian Sea, with a redescription of *Batillipes similis* (Heterotardigrada, Batillipedidae). *Italian Journal of Zoology* **66:** 51-61.

D'ADDABBO GALLO, M., MORONE DE LUCIA, M.R., GRIMALDI DE ZIO, S. 1987. Heterotardigrada of the Amendolara Shoal, High Ionian Sea. Pp. 103–110 *in* 'Biology of Tardigrades'. Ed. R. Bertolani. Proceedings of the 4th International Symposium on the Tardigrada. Modena, September 3–5, 1985. Collana U.Z.I. Selected Symposia and Monographs 1.

DE ZIO, S. 1962. Descrizione di *Batillipes annulatus* n. sp. e note su *B. pennaki* Marcus nuovo rinvenimento nel Mediterraneo (Heterotardigrada) *Annuario dell'Istituto e Museo di Zoologia della Università di Napoli* **14:** 1–7.

D'HONDT, J. -L. 1970. Gastrotriches, Kinorhynques, Rotifères, Tardigrades. Inventaire de la Faune marine de Roscoff. Ed. Station Biologique Roscoff. Pp. 1–29.

FENCHEL, T., 1969. The ecology of marine microbenthos IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the macrofauna communities with special reference to the ciliated protozoa. *Ophelia* **6:** 1–182.

FENCHEL, T., JANSSON, B. O. & THUN, W. V. 1967. Vertical and horizontal distribution of the metazoan microfauna and of some physical factors in a sandy beach in the northern part of the Oresund. *Ophelia* **4:** 227–243.

FIZE, A. 1957. Description d'une espèce nouvelle de Tardigrade *Batillipes carnonensis* n. sp. *Bulletin de la Société Zoologique de France* **82:** 430–433.

FIZE, A. 1963. Contribution a l'étude de la microfaune des sables littoraux du Golfe d'Aigues-Martes. *Vie et Milieu* **14:** 669–774.

FLEEGER, J. W., 1978. Free-living invertebrates. Phylum Tardigrada. Pp. 224 *in* 'An Annotated Checklist of the Biota of the Coastal Zone of South Carolina'. Ed. R. G. Zingmark. University of South Carolina Press: Columbia.

FREIDRICH, H. 1963. Kurze Notizen sur marinen Fauna der Aussenweser. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* **8:** 109

GAUGLER, M. S. & NELSON, D. R. 1997. Marine interstitial tardigrades of Dauphin Island, Alabama [USA]. *Association of Southern Biologists Bulletin* **44:**112.

GAUGLER, M.S. & ROMANO, F. A. 1995. A preliminary survey of marine sand tardigrades of Dauphin Island, Alabama. *Journal of the Alabama Academy of Science* **66:**14.

GRIMALDI DE ZIO, S. & D'ADDABBO GALLO, M. 1975. Reproductive cycle of *Batillipes pennaki* Marcus (Heterotardigrada) and observations on the morphology of the female genital apparatus. VII European Marine Biology Symposium Sorrento (Naples) 1973. *Pubblicazioni Stazione Zoologica di Napoli*, Supplement **39:** 212–225.

GRIMALDI DE ZIO, S., D'ADDABBO GALLO, M. & MORONE DE LUCIA, M. 1983. Marine tardigrades of the 'Secca dell Armeleia' (Ionian Sea), and redescription of *Raiarctus colurus* Renaud-Mornant 1988 (Heterotardigrada). *Oebalia* **9:** 33–42.

GRIMALDI DE ZIO, S., D'ADDABBO GALLO, M. & MORONE DE LUCIA, M. & GRIMALDI, P., 1980. Ulteriori dati sui Tardigradi del mesopsammon di alcune spiagge pugliesi. *Thalassia Salentina* **10:** 45–65.

GRIMALDI, DE ZIO, S., D'ADDABBO GALLO M., MORONE DE LUCIA, M. R., SANDULLI, R., D'ADDABBO, R., FAIENZA, M. G. & PIETANZA, R. 1999. First data on subtidal Meiofauna of Termiti Islands. *Biologia Marina Mediterranea* **6:** 380–382.

GRIMALDI, DE ZIO, S., MORONE DE LUCIA, M. R., D'ADDABBO GALLO, M. & GRIMALDI, P. 1979. Osservazioni su alcuni tardigradi di una spiaggia publiese e descrizione di *Batillipes adriaticus* sp. nov. (Heterotardigrada). *Thalassia Salentina* **9:** 39–50.

GUÉRIN, M. 1960. Observations écologiques sur *Convoluta roscoffensis* Graf. *Cahiers de Biologie Marine* **1:** 205–220

HAY, W. P. 1917. A new species of bear-animacule from the coast of North Carolina. *Proceedings of the United States National Museum* **53**(2203): 251–254.

HUMMON, W. D. 1994. Trans and Cis-Atlantic distributions of three marine heterotardigrades. *Transactions of the American Microscopical Society* **113:** 333–342.

JÄGERSTEN, G. 1952. Studies on the morphology, larval development, and biology of *Protodrilus*. *Zoologiska Bidrag från Uppsala*. **29:** 425–512

KARLING, T. G. 1954–1955. Uber einige Kleintiere des Meeressandes des Nordsee-Ostsee-Gebietes. *Arkiv für Zoologie* **7:** 241–249.

KING, C. E. 1962. The occurrence of *Batillipes mirus* Richters (Tardigrada) in the Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean* **12:** 201–203.

KRISTENSEN, R. M. 1976. On the fine structure of *Batillipes noerrevangi* Kristensen 1976. 1. Tegument and moulting cycle. *Zoologischer Anzeiger* **197:** 129–150.

KRISTENSEN, R. M. 1978. Notes on marine Heterotardigrada. 1. Description of two new *Batillipes* species, using the electron microscope. *Zoologischer Anzeiger* **200:** 1–17

KRISTENSEN, R. M. 1982. The first record of cyclomorphosis in Tardigrada based on a new genus and species from Arctic meiobenthos. *Zeitschrift für Zoologische Systematik und Evolutionforschung* **20:** 249–270.

KRISTENSEN, R. M. & HIGGINS, R. P. 1984. A new family of Arthrotardigrada (Tardigrada: Heterotardigrada) from the Atlantic Coast of Florida. *Transactions of the American Microscopical Society* **103:** 295–311.

LINDGREN, E. W. 1971. Psammolittoral marine Tardigrades from North Carolina and their conformity to worldwide zonation patterns. *Cahiers de Biologie Marine* **12:** 481–96.

McGINTY, M. M. 1969. *Batillipes gilmartini*, a new marine tardigrade from a California beach. *Pacific Science* **23:** 394–396.

McGINTY, M. M. & HIGGINS, R. P. 1968. Ontogenetic variation of taxonomic characters of two marine tardigrades with the description of *Batillipes*

bullacaudatus n. sp. *Transactions of the American Microscopical Society* **87:** 252–262.

McINTYRE, A. D. & MURISON, D. J. 1973. The meiofauna of a flatfish nursery ground. *Journal of the Marine Biological Association of the United Kingdom* **53:** 93–118.

McKIRDY, D. J. 1975. *Batillipes* (Heterotardigrada): comparison of six species from Florida (USA) and a discussion of taxonomic characters within the genus. *Memorie dell'Istituto Italiano di Idrobiologia Pallanza* **32** suppl.: 177–223.

MACKNESS, B. S. 1999. New records of marine tardigrades (Arthrotardigrada) from Victoria. *Proceedings of the Royal Society of Victoria* **111:** 303–308.

MARCUS, E. 1929. Tardigrada. *In* 'Klassen und Ordnungen des Tierreichs', Bnd 5, Abt. IV, Buch 3. Ed. H. G. Bronn. Leipzig. 608p.

MARCUS, E. 1946. *Batillipes pennaki*, a new marine Tardigrada from the north and south American Atlantic coast. *Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo* **2:** 1–3.

MATARRESE, A., TURSI., A., GRIMALDI DE ZIO, S., GALLO D'ADDABBO, M & MORONE DE LUCIA, M. R. 1996. Ulteriori osservazioni sul Macrobenthos (Echinodermi e Tunicati) e sul meiobenthos delle Isole Eoile. Pp 333–350 *in* 'Caratterisazione Ambientale Marina del Sistema Eolie e dei Bacini Limitrofi de Cefalù e Gioia'. Ed. M. F. Faranda & P. Povero. EOCUMM 95.

MORONE DE LUCIA, R. M., D'ADDABBO, D. & GRIMALDI DE ZIO, S. 1988. Descrizione di due nuove specie di Batillipedidae (Tardigrada, Heterotardigrada). *Cahiers de Biologie Marine* **29:** 361–373.

PAPI, F. 1952. Su alcuni Tardigradi raccolti nell' Italia centrale. *Atti della Società Toscana di Scienze Naturali, Processi Verbali e Memorie, Serie B* **59:** 116–118.

PETELINA, O. YU. & TCHESUNOV, A. V. 1983. A new representative of the fauna of the White Sea *Hypsibius apelloefi* (Tardigrada). *Zoologischeskii Zhurnal* **62:** 177–20.

PLESA, C. 1963. Etude sur la faune interstitielle littorale de la Mer Noire. *Vie et Milieu* **14:** 775–813.

POLLOCK, L. W. 1970a. *Batillipes dicrocercus* n. sp. *Stygarctus granulatus* n. sp., and other Tardigrada from Woods Hole, Massachusetts, USA. *Transactions of the American Microscopical Society* **89:** 38–52.

POLLOCK, L. W. 1970b. Distribution and dynamics of interstitial Tardigrada at Woods Hole, Massachusetts, U.S.A. *Ophelia*. **7:** 145–166.

POLLOCK, L. W. 1971. On some British marine Tardigrada including two new species of *Batillipes*. *Journal of the Marine Biological Society of the United Kingdom* **51:** 93– 103.

POLLOCK, L. W. 1975. The role of three environmental factors in the distribution of the interstitial tardigrade *Batillipes mirus* Richters. *Memorie dell'Istituto Italiano di Idrobiologia Pallanza* **32** suppl.: 305–324.

POLLOCK, L. W. 1989. Marine interstitial Heterotardigrada from the Pacific Coast of the United States, including a description of *Batillipes tridentatus* n. sp. *Transactions of the American Microscopical Society* **108:** 169–189.

PURASJOKI, K. 1953. Zwei verbesserte Apparate zum Auffangen von Kleintieren des See- und Meeresbodens. *Archivum Societatis Zoologicae-Botanicae Fennicae 'Vanamo'* **8:** 110–114.

RAO, G. C. 1971. On two species of marine interstitial Tardigrada from the east coast of India. *Proceedings of the Indian Academy of Sciences, Section B* **73**(2)**:** 53–57.

RAO, G. C. & GANAPATI, P. N. 1968. The interstitial fauna inhabiting the beach sands of Waltair coast. *Proceedings of the National Institute of Sciences in India. Part B Biological Sciences* **34:** 82–125.

REMANE, A. 1940. Einführung in die zoologische Ökologie der Nord- und Ostsee. *In* 'Tierwelt Nord- und Ostsee'. Eds G. Grimpe and E. Wagler. Lieferung **34:** 1–238.

RENAUD-DEBYSER, J. 1956. Répartition de deux Tardigrades *Batillipes mirus* Richters et *Stygarctus bradypus* Schulz dans un segment de plage du Bassin d'Arcachon. *Compte Rendu de l'Académie des Sciences (Paris)* **243:** 1365–1379.

RENAUD-DEBYSER, J. 1959. Sur quelques Tardigrades du Bassin D'Arcachon. *Vie et Milieu* **10:** 135–146.

RENAUD-DEBYSER, J. & SALVAT, B. 1963. Éléments de prospérité des biotopes des sédiments meubles intertidaux et écologie de leurs populations en microfaune et macrofaune. *Vie et Milieu* **14:** 463–550.

RENAUD-MORNANT, J. 1979. Tardigrades marins de Madagascar. 1. Halechiniscidae et Batillipedidae. *Bulletin du Muséum National d'Histoire Naturelle, Paris* **1:** 257–277.

RENAUD-MORNANT, J. & JOUIN, C. 1965. Note sur la microfaune du fond à *Amphioxus* de Graveyron et d'autres stations du Bassin d'Arcachon. *Actes de la Société Linnéene de Bordeaux* **102:** 1–7.

RENAUD-MORNANT, J. & SERENE, P. 1967. Note sur la microfaune de la côte orientale de la Malaisie. (Gastrotriches, Annélides, Tardigrades et Copépodes Harpacticides). *Cahiers du Pacifique* **11:** 51–73.

RHO, H. S., MIN, B. H. & CHANG, C. Y. 1999. Taxonomic study of Marine Tardigrades from Korea. 1. Genus *Batillipes* (Heterotardigrada: Batillipedidae). *The Korean Journal of Systematic Zoology* **15**(1)**:** 107–118.

RICHTERS, F. 1909. Tardigraden Studien. *Berichte der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt A.M.* **40:** 28–45.

RIEMANN, F. 1966. Die Verbreitung der interstillen Fauna im Elbe-Aestuar. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* **2:** 114–123.

RIGGIN, G. T. 1962. Tardigrada of southwest Virginia: With the addition of a description of a new species from Florida. *Virginia Agricultural Experimental Station Technical Bulletin* **152:** 1–145.

RUDESCU, L. 1964. Tardigrada. In *Fauna Republicii Populare Romine* **7:** 1–400.

SCHMIDT, P. 1969. Die quantitative Verteilung und Populationsdynamik des Mesopsammons am Gezeiten-Sandstrand der Nordseeinsel Sylt II. Quantative Verteilung und Populationsdynamik einzelner Arten. *Internationale Revue der gesamten Hydrobiologie* **54:** 95–174.

SCHULZ, E. 1955. Studien an marinen Tardigraden. *Kieler Meeresforschung* **11:** 73–79.

SWEDMARK, B. 1956(a). Nouveaux gastrotriches Macrodasyoïdes de la région de Roscoff. *Archives de Zoologie Expérimentale et Générale* **94:** 43–57.

SWEDMARK, B. 1956(b). Etude de la microfaune des sables marins de la région de Marseille. *Archives de Zoologie Expérimentale et Générale. Notes et Revue* **2:** 70–95.

TAMBS-LYCHE, H. 1939-1940. Marine Tardigraden bei Bergen. *Bergens Museums Årbok 1939–40, Naturvitenskabelig rekke* **5:** 1–5.

TCHESUNOV, A. V. & MOKIEVSKY, V. O. 1995. A new marine tardigrade, *Batillipes crassipes* sp. nov., from the Japan Sea (Tardigrada Arthrotardigrada, Batillipedidae). *Cahiers de Biologie Marine* **36:**153–157.

VALKANOV, A. 1950. *Echiniscoides sigismundi* (M. Schultze) ot Czerno More. *Trudy Murmanskogo Morskogo Biologicheskogo Instituta* **15:** 181–186.

VALKANOV, A. 1954. Czernomorskye Tardigradi. Die Tardigraden des Schwarzen Meeres. *Sofücki universitet* **48:** 59–61.

VILLORA-MORENO, S. & GRIMALDI DE ZIO, S. 1993. Redescription and ecology of *Batillipes phreaticus* Renaud-Debyser, 1959 (Arthrotardigrada, Batillipedidae) in the gulf of Valencia (Western Mediterranean). *Cahiers de Biologie Marine* **34:** 387–399.